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## Diet of two icefish species from the South Shetland Islands and Elephant Island, *Champsocephalus gunnari* and *Chaenocephalus aceratus*

Received: 4 August 2003 / Accepted: 21 October 2003 / Published online: 3 December 2003  
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**Abstract** The summer diet of two species of icefishes (Channichthyidae) from the South Shetland Islands and Elephant Island, *Champsocephalus gunnari* and *Chaenocephalus aceratus*, was investigated from 2001 to 2003. *Champsocephalus gunnari* fed almost exclusively on krill (*Euphausia superba*) in all years. The importance of other taxa (*Themisto gaudichaudii*, mysids, myctophids) in the diet was negligible. The average feeding rate of *Champsocephalus gunnari* inferred from an exponential gastric evacuation model was between 1.0 and 1.5% body weight per day. Most of the stomachs of *Chaenocephalus aceratus* were empty. Stomachs with food contained mainly krill, mysids and fish. Among the fish taken, locally abundant species formed the bulk of the diet: *Gobionotothen gibberifrons* in 2001, *Lepidonotothen larseni* and *Champsocephalus gunnari* in 2002 and *L. larseni* in 2003. An ontogenetic shift in feeding preference of *Chaenocephalus aceratus* was observed: fish smaller than 30 cm fed on krill and mysids, while larger animals relied primarily on fish.

### Introduction

The Antarctic fish fauna is dominated by the perciform suborder Notothenioidei, which comprises the majority

of species in shelf waters down to 500 m depth and accounts for more than 90% of the fish biomass in most regions of the Southern Ocean (Eastman and Clarke 1998). Among the eight notothenioid families, icefishes (Channichthyidae) are peculiar in that their blood does not contain haemoglobin (Ruud 1954).

The South Shetland Islands are located north of the Antarctic Peninsula. They are part of the low-Antarctic zoogeographical province, or seasonal pack-ice zone (Kock 1992). Krill (*Euphausia superba*) is considered the key species of the marine food web in this province (Hempel 1985; Verity and Smetacek 1996). Many demersal fish species depend directly or indirectly on krill (Gröhsler 1992).

Only four of the 15 Antarctic icefish species (Eastman and Eakin 2000) are found in some abundance in the low-Antarctic Province. Two of these, mackerel icefish (*Champsocephalus gunnari*) and Scotia Sea icefish (*Chaenocephalus aceratus*), are among the most abundant fish species on the continental shelf of Elephant Island and the South Shetland Islands (Kock 1998; Kock and Stransky 2000). Some biological features of the two species have been well-documented, including reproduction (Kock 1981; Kock and Kellermann 1991; Kock et al. 2001; Kock and Jones 2003) and the composition of their diet (Taverdieva and Pinskaya 1980; Kock 1981, 1982; Sosinski 1985; Kozlov et al. 1988; McKenna 1991; Takahashi and Iwami 1997; Kock and Jones 2003). However, these studies either concentrated on a limited number of samples from a limited number of stations and/or on a comparatively small area of investigation. The only extensive analysis available is an early winter study conducted around Elephant Island in May/June 1986 by Gröhsler (1992).

In the investigation reported here, we present data on the stomach contents of *Champsocephalus gunnari* and *Chaenocephalus aceratus* collected over the whole shelf in three consecutive years in order to provide a more comprehensive picture of the summer diets and feeding habits of these species.

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## Materials and methods

Material was collected during three demersal finfish surveys conducted by the U.S. AMLR (Antarctic Marine Living Resources) programme in 2001 and 2003 and the German Antarctic Marine Living Resources Programme in 2002 under the auspices of the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) at Elephant Island and the South Shetland Islands. Samples were taken aboard R.V. "Yuzhmorgeologiya" from 12 to 31 March 2001, aboard R.V. "Polarstern" from 29 January to 19 February 2002 and aboard "Yuzhmorgeologiya" from 7 March to 4 April 2003 from the water around Elephant Island and the South Shetland Islands. The distribution of stations where material was collected is provided in Fig. 1a–c. Fish were caught during daylight hours using a commercial size bottom trawl. Fishing depths ranged from 50 m to 500 m. A detailed description of the trawling operations is provided in Jones et al. (2001, 2003) and Kock et al. (2002). The number of samples per depth stratum collected during the cruises is shown in Table 1. Whenever the number of fish caught was sufficient, at least 40 (2001) or 30 (2002, 2003) individuals of *Champsocephalus gunnari* and *Chaenocephalus aceratus* were collected on each station. The samples covered the complete spectrum of length ranges obtained from both species.

The following data were recorded for each individual fish directly after capture:

- length (total length to the nearest centimeter below);
- sex, maturity (according to a five-point scale: Kock and Kellermann 1991);
- total weight (to the next gram below, by means of an electronic scale);
- gonad weight in adult fish;
- wet weight of the stomach.

Stomachs collected in 2001 were frozen immediately after capture for further analysis in the home laboratory. Stomachs collected in 2002 and 2003 were analysed on board. Stomach fullness was classified according to a six-point scale: 0 (empty), 1 (>0–24% full), 2 (25–49% full), 3 (50–100% full), 4 (>100% full), 5 (regurgitated). The degree of digestion (DOD) was estimated following a four-point scale: 1 (fresh—no signs of digestion), 2 (slightly digested), 3 (advanced stage of digestion) and 4 (heavily digested).

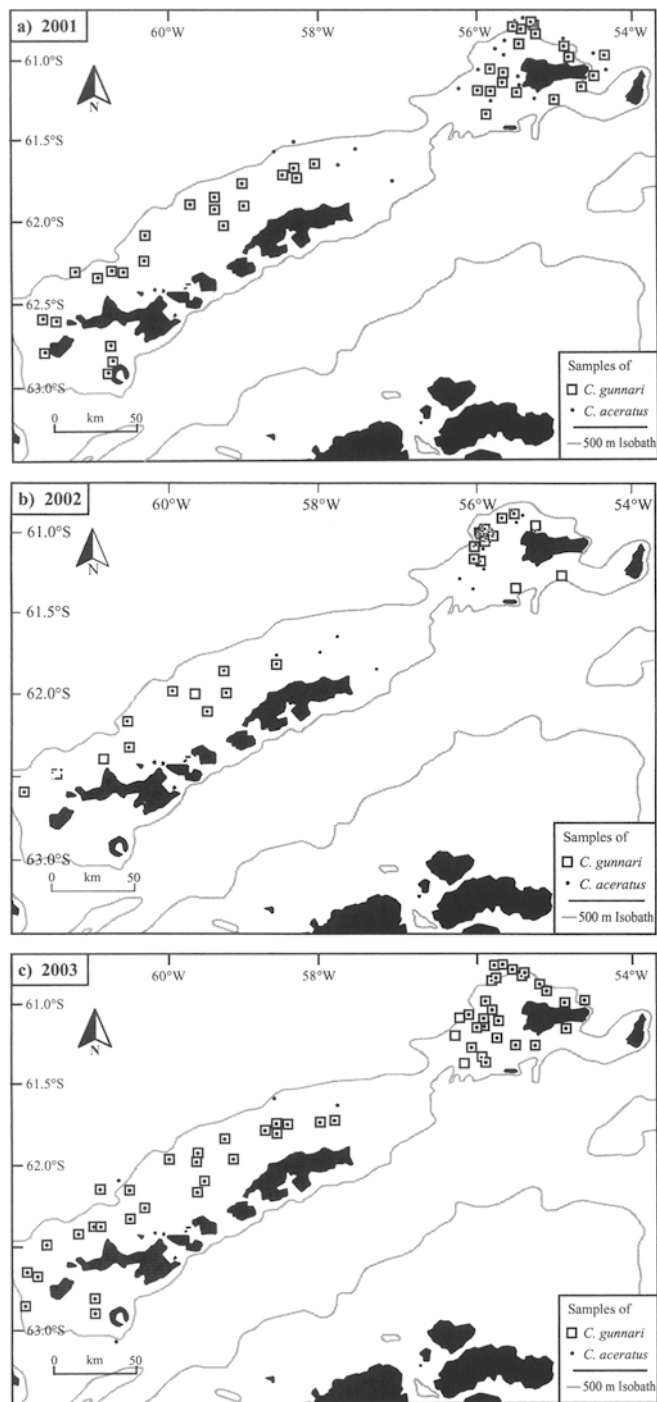
The composition of the stomach contents from both species was identified to the lowest taxon possible by means of a stereo microscope. Food composition in all years was expressed as frequency of occurrence. In 2001, items in each prey category were counted, whenever possible. In cases of advanced decay, the minimum number of crustaceans in each sample was estimated as half the number of eyes detected. Total weight of the stomach content and wet weight of each fraction of the stomach content were determined to an accuracy of 0.1 g. In 2002 and 2003, accuracy was only to the nearest gram below, food fractions were not weighed, and items were not counted.

Data collected in 2001 allowed the calculation of the proportion of total food weight for each prey taxon as well as their dietary coefficient,  $Q$  (Hureau 1969):

$$Q = h_i * g_i; \quad (1)$$

where  $Q$  is the dietary coefficient,  $h_i$  is the relative abundance and  $g_i$  is the relative weight of the prey category  $i$ . Based on this index, prey items can be separated into three classes:  $Q > 200$  (main prey),  $200 > Q > 20$  (secondary prey) and  $Q < 20$  (occasional prey). The calculation of  $Q$  values for *Champsocephalus gunnari* turned out to be dispensable since the diet of this species was dominated by one prey species only.

Relative feeding rates of *C. gunnari* were calculated based on a gastric evacuation model. Since there is little knowledge about the process of digestion in channichthyids and experimental data on feeding rates of notothenioids are scarce and somewhat



**Fig. 1** Positions of sampling stations for *Champsocephalus gunnari* and *Chaenocephalus aceratus* in 2001 (a), 2002 (b) and 2003 (c). Stations at which the stomachs of *Champsocephalus gunnari* were analysed are indicated by open squares; stations at which *Chaenocephalus aceratus* was sampled are shown as black dots

inconsistent (Kock 1992), a model of gastric evacuation was chosen which was as simple as possible. Elliott and Persson (1978) proposed an exponential model in a generalized form. It was found to describe the evacuation process in most fish species, though it has been refined by a number of authors (e.g. Persson 1986; Andersen 1999, 2001). Hop and Tonn (1998) showed that this model was applicable to cold-adapted polar cod (*Boreogadus saida*). Results

**Table 1** Number of stomachs sampled from *Chamsocephalus gunnari* and *Chaenocephalus aceratus* in each depth stratum at the South Shetland Islands

Depth Stratum (m)	2001		2002		2003	
	<i>C. gunnari</i>	<i>C. aceratus</i>	<i>C. gunnari</i>	<i>C. aceratus</i>	<i>C. gunnari</i>	<i>C. aceratus</i>
> 50–100	133	46	31	10	143	68
> 100–200	622	347	356	254	499	414
> 200–300	124	133	34	251	101	232
> 300–400	39	58	–	64	65	52
> 400–500	–	11	–	18	14	38
Total	918	595	421	597	822	804

from experimental studies on other notothenioids, e.g. *Pagothenia borchgrevinki* (Montgomery et al. 1989) or *Harpagifer antarcticus* (Boyce et al. 2000), agree with an exponential mode of stomach evacuation.

Feeding rate was assumed to equal stomach evacuation rate  $R$  which was calculated as follows:

$$R = a * e^{bT} \text{ (Elliott and Persson 1978);} \quad (2)$$

where  $R$  is the gastric evacuation rate and  $a$  and  $b$  are absolute terms.

For the purpose of this paper,  $a$  and  $b$  were considered to be close to values determined for polar cod.  $R$  was calculated with  $a = 0.018$  and  $b = 0.14$  (Hop and Tonn 1998):

$$R = 0.018 * e^{0.14} = 0.0207 \quad (3)$$

Mean daily consumption ( $R'$ ) and relative daily feeding rate ( $r'$ ) were calculated for each 5-cm length class of the *C. gunnari* investigated:

$$R'(L) = 24 * \overline{W_{SC}}(L) * 0.0207; \quad (4)$$

where  $R'(L)$  is the consumption in grams per day, and  $\overline{W_{SC}}(L)$  is the mean stomach content wet weight in grams in each length class  $L$ ;

$$r'(L) = 100 * 24 * \frac{\overline{W_{SC}}(L)}{\overline{TW}(L)} * R; \quad (5)$$

where  $r'(L)$  is the relative feeding rate in percentage body weight per day, and  $\overline{TW}(L)$  is the mean total weight of the fish in grams in each length class  $L$ .

The resulting daily rations were taken to estimate the total stock's consumption of krill in the area of investigation. In order to perform these calculations, we used the data available on stock sizes from 2001 (Jones et al. 2001) and 2002 (Kock et al. 2002); data for 2003 were not yet available. Since the daily ration differed between length classes, the consumption was first calculated for each length class separately before adding up the amounts of krill consumed in each length class. The total number of individuals per length group in the population was calculated as follows:

$$N_T(L) = \frac{B_T * N_C(L)}{B_C}; \quad (6)$$

where  $N_T(L)$  is the total stock number of individuals in length group  $L$ ,  $B_T$  is the standing stock biomass in the area of investigation,  $N_C(L)$  is the number of individuals caught in length group  $L$  and  $B_C$  is the biomass of the total catch of *C. gunnari*.

The daily krill consumption of the standing stock was then estimated:

$$B_K = \sum \frac{R'(L) * P_K(L) * N_T(L)}{10^3}; \quad (7)$$

where  $B_K$  is the biomass of krill consumed by the standing stock of *C. gunnari* per day in metric tonnes (mt), and  $P_K(L)$  is the proportion of krill in the diet of length group  $L$ .

Most of the stomachs of *Chaenocephalus aceratus* were empty. Consequently, no feeding rates were calculated for these fish because gastric evacuation models usually assume a continuous food intake.

## Results

### *Chamsocephalus gunnari*

#### *Stomach fullness and degree of digestion*

In samples collected in 2001, the proportion of empty stomachs was low (10%), and few appeared to be regurgitated (1%). Most of the stomachs (71%) were in filling degree 2 or higher. In 2002, the proportion of empty stomachs was considerably higher (27%). The majority of stomachs (50%) were in filling degree 2 or higher, and no stomachs were found to be regurgitated. In 2003, the distribution was somewhat intermediate: the proportion of empty stomachs was higher than in 2001 but lower than the preceding year (17%). The proportion of stomachs which was at least in filling degree 2 was also in-between the two other years (62%) (Fig. 2a).

In 2001, most of the stomach contents (75%) were considerably digested (DOD 3 or 4). The proportion of stomach contents that was fresh or only slightly digested (DOD 1 or 2) was higher in 2002 and 2003 (50% and 52%, respectively), when no stomach contents were judged to be heavily digested (Fig. 2b).

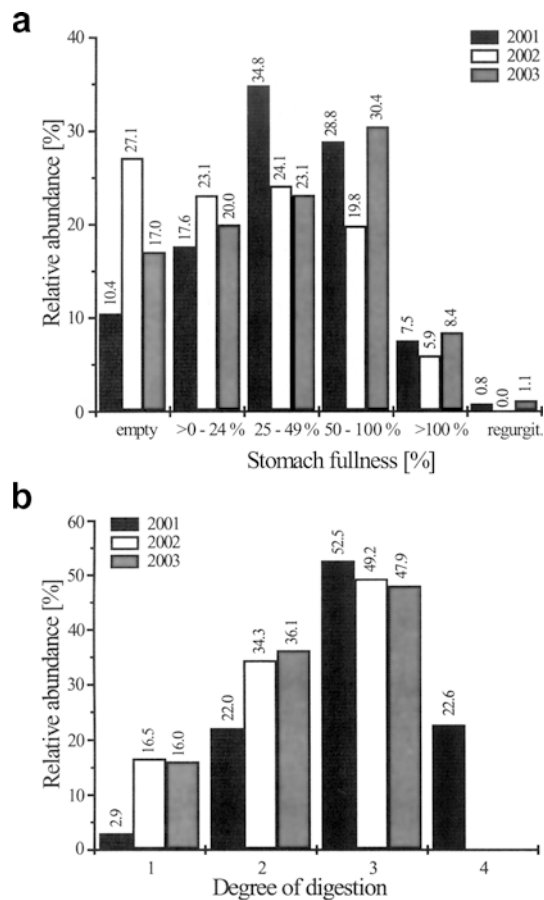
#### *Stomach content weight*

Overall mean stomach content weight in 2001 was 6.8 g (SD = 9.31). It was lower in 2002 (5.3 g; SD = 8.75), while in 2003 it was as high as 8.3 g. (SD = 10.65). Maximum stomach content weight was 75 g in 2001, 65 g in 2002 and 74 g in 2003.

Stomach content weight was positively correlated with fish length. The relationship of stomach content weight to total length of fish approximately followed an exponential function of the form:

$$W_{st} = a * e^{bTL}; \quad (8)$$

where  $W_{st}$  is the median value of the stomach content weight at any given length, TL is the total length of fish and  $a$  and  $b$  are constants. Non-linear regression analysis was performed separately on each year's data. The results are shown in Table 2. As an example, Fig. 3 illustrates the observed relationship and the distribution of data in 2002.



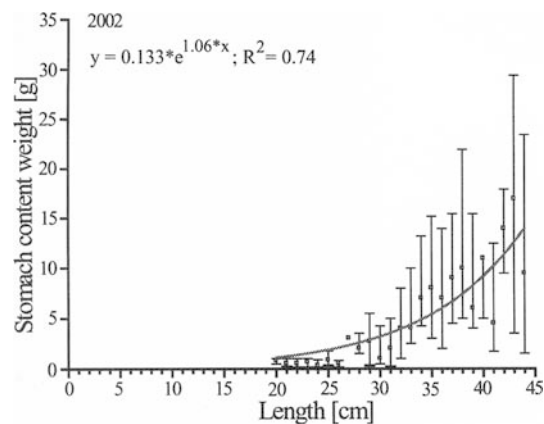
**Fig. 2** *Champsocephalus gunnari*—distribution of stomach fullness (a) and degrees of digestion (b) in 2001 (dark columns), 2002 (white columns) and 2003 (grey columns). The percentages of abundance of stomachs in each category are indicated above the columns

**Table 2** Results of non-linear regression analysis on the relationship between stomach content weight and length of *C. gunnari* in 2001–2003. Regression function:  $y = axe^{bx}$

Year	a	b	R <sup>2</sup>
2001	0.425	0.089	0.75
2002	0.133	0.106	0.74
2003	0.205	0.101	0.59

### Feeding rates

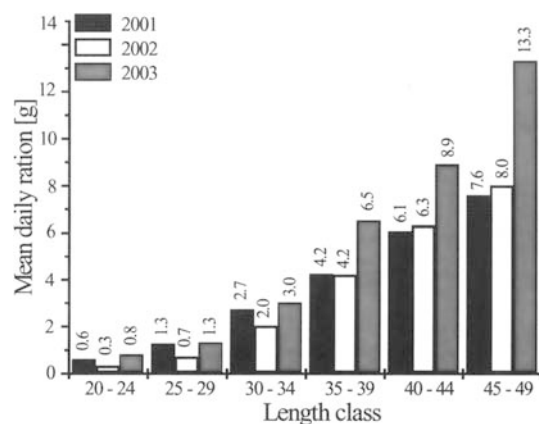
Average daily rations and relative feeding rates per length class in all years are provided in Table 3 and Fig. 4. Fish smaller than 20 cm and larger than 49 cm were not taken into consideration due to the limited number of individuals caught in these length classes. The mean daily ration increased with increasing body size. In 2001, it was 0.6 g per day in the 20- to 24-cm length class and 7.6 g per day in the 45- to 49-cm length class. In 2002 and 2003, the range was from 0.3 g to 8.6 g and 0.8 g to 13.3 g, respectively (Fig. 4). Overall mean daily ration was 3.4 g in 2001, 2.5 g in 2002 and 4.1 g in 2003. The relative feeding rate was constant over the observed



**Fig. 3** *Champsocephalus gunnari*—median values of stomach content wet weight against length of fish with regression line and equation. Error bars indicate 25% and 75% percentiles

**Table 3** Mean daily feeding rates ( $r'$ , in percentage body weight) in each length class of *C. gunnari* from the South Shetland Islands 2001–2003 ( $n$  number of stomachs with food per length group)

Length class (cm)	2001		2002		2003	
	n	$r'$ (%)	n	$r'$ (%)	n	$r'$ (%)
20–24	137	0.8	100	0.5	111	1.2
25–29	179	1.0	30	0.6	104	1.1
30–34	70	1.0	76	0.9	204	1.4
35–39	147	1.0	93	1.2	121	1.7
40–44	164	0.9	26	1.1	109	1.7
45–49	66	0.9	12	1.0	11	1.5
Mean	–	1.0	–	1.2	–	1.5



**Fig. 4** *Champsocephalus gunnari*—mean daily rations in grams per day in 5-cm length classes, 2001–2003

length range in 2001, ranging from 0.8% to 1.0% body weight per day in each length group. In the following year, the rates in fish smaller than 30 cm were considerably lower (0.5–0.6%) than in larger animals (0.9–1.2%). Mean rate of food intake in all fish was 1.0% body weight per day in both 2001 and 2002. Higher feeding rates were observed in 2003, when the average feeding rate was 1.5% body weight (Table 3).

The daily rations, together with the total sizes and length compositions of the stocks, enabled the calculation of the total krill consumption of the stock of *C. gunnari* around Elephant Island and the South Shetland Islands in 2001 and 2002. Using the estimated biomass of *C. gunnari* from 2001 (Jones et al. 2001) and 2002 (Kock et al. 2002), we calculated the monthly krill consumption of mackerel icefish stocks to be approximately 1,150 mt in 2001 and 690 mt in 2002 (Table 4).

#### Food composition

The diet of *C. gunnari* consisted of only a few species in all three years. The food composition is provided in Table 5. Krill was by far the most dominant prey item. In 2001, 99% of the stomachs with food contained krill, and 4% contained unidentifiable material, as well as algae and stones. Other food items, such as *Themisto gaudichaudii* (Hyperiididae; 1%), myctophids (1%) and unidentified crustaceans (<1%) were encountered occasionally. Unidentified crustaceans were probably largely krill that were too fragmented by digestion to be identified to species level. *Euphausia superba* also domi-

nated in terms of relative number and stomach content wet weight (each 99%). Samples collected in 2002 and 2003 exhibited a similar range of prey items. Krill was again the dominant prey species which was present in 92% and 91% of the stomachs, respectively. Of the stomachs collected in 2002, 5% contained *T. gaudichaudii*. Other prey items were unidentified fish (1%) and *Euphausia* spp. (1%). Material in 6% of the stomachs was unidentifiable. In 2003, *Thysanoessa macrura* together with other euphausiids were found in some stomachs (8%). *Themisto gaudichaudii* and unidentified amphipods were found in 4% of the stomachs. Unidentified fish (2%) and myctophids (1%) occurred occasionally. Other food items were encountered in less than 1% of the stomachs; 1% of the prey objects were unidentifiable.

#### *Chaenocephalus aceratus*

#### Stomach fullness and degree of digestion

Most of the stomachs collected in 2001 (76%) were empty. The majority of the stomachs containing food (14%) were in filling degree 1 or 2. Few stomachs (2%)

**Table 4** Krill biomass consumed by standing stocks of *C. gunnari* around Elephant Island and the South Shetland Islands in 2001 and 2002

	2001	2002
Standing stock biomass <sup>a</sup> (t)	5,121 (3,402–9,587) <sup>b</sup>	3,019 (1,509–16,787) <sup>b</sup>
Krill consumption (mt/month)	1,149.0 (763.3–2,149.1)	686.3 (343.1–3,816.4)

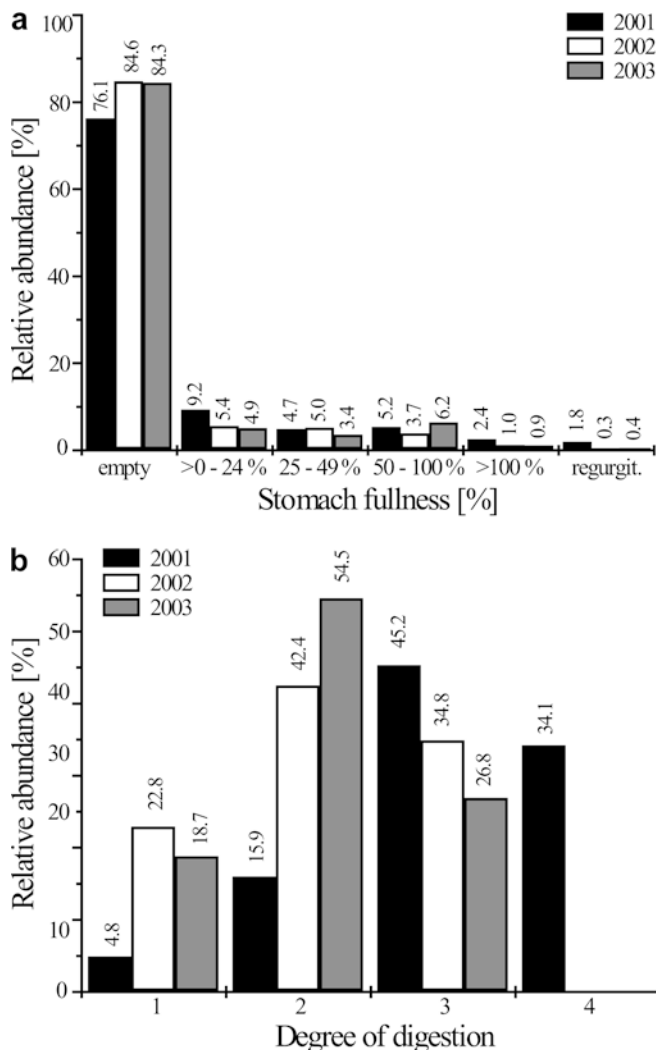
<sup>a</sup>Source: 2001, Jones et al. (2001); 2002, Kock et al. (2002)

<sup>b</sup>75% confidence limits are indicated in brackets

**Table 5** Composition of the diet of *C. gunnari* from the South Shetland Islands 2001–2003: percentage frequencies of occurrence (F%), number (N%) and wet weight (W%)

	2001 (823) <sup>a</sup>			2002 (309) <sup>a</sup>	2003 (682) <sup>a</sup>
	F%	N%	W%	F%	F%
Crustaceans (total)	100.1	99.9	99.3	97.1	102.2
Euphausiacea					
<i>Euphausia superba</i>	98.7	99.3	98.7	91.6	91.2
<i>E. frigida</i>	–	–	–	–	0.3
<i>Euphausia</i> spp.	–	–	–	0.6	3.5
<i>Thysanoessa macrura</i>	–	–	–	–	3.5
Mysidacea					
Mysidacea indeterminate	–	–	–	–	0.1
Amphipoda					
<i>Themisto gaudichaudii</i>	0.7	0.6	0.0	4.9	2.1
Amphipoda indeterminate	–	–	–	–	1.5
Crustacea indeterminate	0.4	–	0.6	0.0	–
Fish (total)	1.2	0.1	0.1	1.0	2.9
Nototherioidei					
<i>Lepidonotothen larseni</i>	–	–	–	–	0.1
Myctophidae					
Myctophidae indeterminate	1.1	0.1	0.1	0.0	0.6
Pisces indeterminate	<0.1	–	–	1.0	2.2
Others (total)	4.3	–	0.6	6.5	1.5
Polychaeta					
Polychaeta indeterminate	–	–	–	–	0.1
Ophiuroidea					
Ophiuridae indeterminate	–	–	–	–	0.1
Unidentified	4.3	–	0.6	6.5	1.3

<sup>a</sup>Number of stomachs with food in each year in brackets



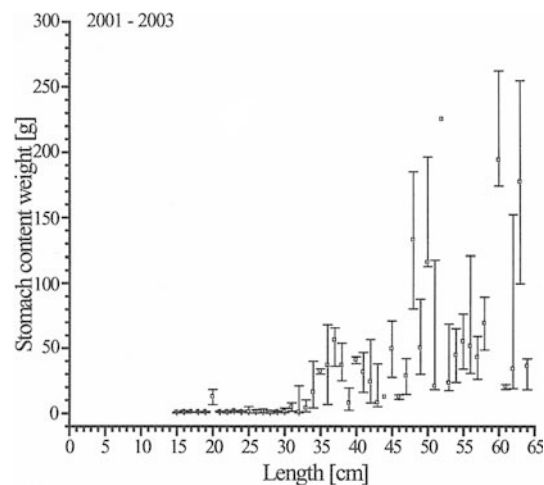
**Fig. 5** *Chaenocephalus aceratus*—distribution of stomach fullness (a) and degrees of digestion (b) in 2001 (dark columns), 2002 (white columns) and 2003 (grey columns). The percentages of abundance of stomachs in each category are indicated above the columns

appeared to be regurgitated. In 2002 and 2003, the proportion of empty stomachs was even higher (85% and 84%, respectively). Most of the stomachs with food (9% and 8%, respectively) were in filling degree 1 or 2, and fewer than 1% showed signs of being regurgitated (Fig. 5a).

A large proportion of the stomach contents sampled in 2001 (79%) was heavily digested (DOD 3 or 4). In 2002 and 2003, the greater proportion of the stomach contents (65%, 73%) was hardly digested at all (DOD 1 or 2), with the remaining portion (35%, 37%) being in an advanced stage of digestion (DOD 3) (Fig. 5b).

#### Stomach content weight

Stomach content wet weight ranged from less than 1 g to approximately 400 g in 2001 and 2002, and up to approximately 160 g in 2003. Mean weights were 20.4 g



**Fig. 6** *Chaenocephalus aceratus*—median values of stomach content wet weight against length of fish. Error bars indicate 25% and 75% percentiles

(SD = 53.07) in 2001, 33.9 g (SD = 72.20) in 2002 and 14.6 g (SD = 30.04) in 2003.

Given the small number of stomachs containing food in each year, we pooled data from all years in order to describe the relationship of stomach content weight with total length of fish. The results are illustrated in Fig. 6. The stomach content weights of fish shorter than 34 cm were below 50 g, increasing very slightly with increasing size of *Chaenocephalus aceratus*. In larger fish, stomach content weights fluctuated heavily, with the largest values occurring in the largest fish ( $\geq 60$  cm). Due to these fluctuations, no appropriate function could be fitted to the data.

#### Food composition

In general, the diet composition of *C. aceratus* consisted of a mix of small crustaceans, mostly krill and mysids, and demersal fish species. The overall composition of the diet is shown in Table 6. The diet composition varied between stations in all three years of investigation. However, the number of stomachs with food per station was too low to conclude any geographic pattern of feeding preference.

In 2001, *Euphausia superba* was the most frequent prey species (56%). However, it accounted for only 10% of the total wet weight of the prey. *Gobionotothen gibberifrons* and unidentified fish were the most important prey items in terms of weight, accounting for 42% and 23% of the diet, respectively. With regard to the small number of filled stomachs obtained, it seemed reasonable to lump all prey species into the two categories 'crustaceans' (krill, mysids and others) and 'fish' when discussing the importance of different fractions of the diet in terms of the dietary coefficient  $Q$ . Accordingly, crustaceans (1,028) and fish (735) could both be ranked as main prey (Table 7).

**Table 6** Composition of the diet of *C. aceratus* from the South Shetland Islands in 2001 and 2002: percentage frequencies of occurrence (F%), number (N%) and wet weight (W%)

	2001 (128) <sup>a</sup>			2002 (90) <sup>a</sup>	2003 (126) <sup>a</sup>
	F%	N%	W%	F%	F%
Crustaceans (total)	72.3	91.5	11.3	68.9	78.6
Euphausiacea					
<i>Euphausia superba</i>	55.5	79.0	10.3	48.9	50.8
Mysidacea					
<i>Antarctomysis maxima</i>	—	—	—	—	12.7
Mysidacea indeterminate	9.2	12.6	0.9	11.1	12.7
Amphipoda					
<i>Themisto gaudichaudii</i>	—	—	—	2.2	—
Amphipoda indeterminate	—	—	—	—	0.8
Crustacea indeterminate	7.6	—	0.1	6.7	1.6
Fish (total)	26.9	7.5	85.3	33.3	19.8
Notothenoidei					
<i>Gobionotothen gibberifrons</i>	5.0	1.7	41.6	—	—
<i>Lepidonotothen larseni</i>	0.8	0.5	2.8	12.2	6.3
<i>L. nudifrons</i>	1.7	0.5	3.8	1.1	2.4
<i>Champscephalus gunnari</i>	3.4	1.0	6.7	7.8	2.4
<i>Chaenocephalus aceratus</i>	2.5	0.7	7.2	—	0.0
Channichthyidae indeterminate	—	—	—	1.1	—
<i>Parachaenichthys charcoti</i>	—	—	—	1.1	—
<i>Harpagifer antarcticus</i>	—	—	—	—	1.6
Myctophidae					
Myctophidae indeterminate	1.7	—	—	—	—
Trichiuroidei					
Gempylidae indeterminate	—	—	—	1.1	—
Pisces indeterminate	11.8	3.1	23.1	8.9	7.1
Unidentified	4.2	—	1.5	1.1	4.8

<sup>a</sup>Number of stomachs with food in brackets

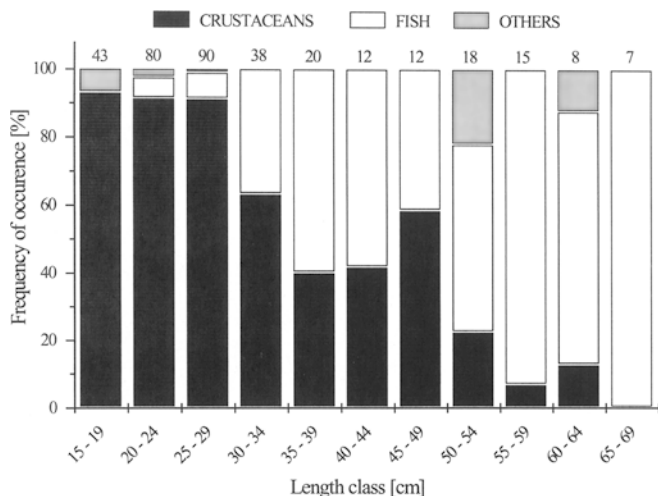
**Table 7** Dietary coefficient *Q* of different prey items of *C. aceratus* from the South Shetland Islands in 2001. *Q* was calculated separately for smaller (< 30 cm) and larger fish (≥ 30 cm), and for all specimens

	< 30 cm	≥ 30 cm	All
Crustaceans (total)	7,811.0	441.6	1,027.8
Euphausiacea			
<i>Euphausia superba</i>	5,545.8	369.1	814.5
Mysidacea			
<i>Antarctomysis maxima</i>	84.3	—	2.0
Mysidacea indeterminate	22.1	1.9	3.8
Fish (total)	12.2	738.8	735.4
Notothenoidei			
<i>Gobionotothen gibberifrons</i>	—	73.4	70.3
<i>Lepidonotothen larseni</i>	—	1.4	1.3
<i>L. nudifrons</i>	—	1.9	1.8
<i>Champscephalus gunnari</i>	12.2	4.5	6.5
<i>Chaenocephalus aceratus</i>	—	5.5	5.2
Myctophidae			
Myctophidae indeterminate	—	1.7	1.6
Pisces indeterminate	—	75.9	72.7

In 2002 and 2003, food items were registered by frequency of occurrence only. In 2002, crustaceans (69%) and fish (33%) showed a distribution similar to 2001. Crustaceans were mostly krill (49%), mysids (11%) and unidentified crustaceans (7%). Among the fish, *Lepidonotothen larseni* (12%), unidentified fish (9%) and *Champscephalus gunnari* (8%) were found most frequently. Other fish species only occurred sporadically.

In 2003, the proportion of crustaceans in the diet (79%) was significantly higher than in the two preceding years. *E. superba* was taken most often (51%), followed by *Antarctomysis maxima* (12.7%) and unidentified mysids (12.7%). Other crustaceans were of minor importance. Fish occurred in 20% of the stomachs with food. *L. larseni* (6%) and *L. nudifrons* (2%) were taken most often. *Harpagifer antarcticus* was encountered occasionally. Fish in 7% of the stomachs could not be identified to species level.

There was a significant change in the diet from smaller to larger *Chaenocephalus aceratus* (Fig. 7). The overwhelming proportion of the stomach contents of fish shorter than 30 cm consisted of crustaceans, predominantly krill and mysids. A change in the composition of the diet was apparent when *C. aceratus* became larger than 30 cm. These older *C. aceratus* gradually relied more and more on a fish diet, and in those larger than 50 cm, only a few stomachs contained crustaceans in addition to prey fish. Fish found in the stomachs were primarily those notothenioids that were also found to be abundant in trawl catches, such as *Champscephalus gunnari*, *Gobionotothen gibberifrons*, *Chaenocephalus aceratus*, *Lepidonotothen nudifrons* and *L. larseni*. In terms of the dietary coefficient *Q*, crustaceans were the only notable prey (7,811) in *C. aceratus* shorter than 30 cm in 2001, and the importance of fish (12) was negligible. In animals 30 cm or longer, fish was the most important prey item (739), and despite their low proportional weight, crustaceans could as well be classified as main prey (442) (Table 7).



**Fig. 7** *Chaenocephalus aceratus*—frequency of occurrence of prey items per 5-cm length class. Columns represent pooled data from 3 years of investigation (2001–2003). The number of stomachs with food in each length class is provided above the columns

## Discussion

### *Champsocephalus gunnari*

#### Food composition

Krill (*Euphausia superba*) seems to be more or less the exclusive prey species of *C. gunnari* in the Elephant Island/South Shetland Islands region. While this has been demonstrated earlier by Taverdieva and Pinskaya (1980), Kock (1981), Kozlov et al. (1988) and Takahashi and Iwami (1997), these studies were either confined to a small area of investigation or were limited in the number of samples investigated. Gröhsler (1992) reported a broader range of prey items at Elephant Island in May/June 1986. It is possible that *C. gunnari* switched to a more diverse prey in order to compensate for a lower availability of krill since krill biomass in the area is usually substantially lower during the winter (Siegel 2000).

The availability of krill is quite variable in the area of distribution of mackerel icefish. High densities of *E. superba* are usually found in the southern part of the Scotia Arc, Elephant Island, the South Shetland Islands and the Antarctic Peninsula during austral summer, whereas krill abundance fluctuates significantly between years at South Georgia (Siegel 2000). In the latter area, the proportion of krill in the diet of *C. gunnari* varied considerably between different sampling years (Kozlov et al. 1988; McKenna 1991; Kock et al. 1994; Barrera-Oro et al. 1997; Kock and Everson 2003).

Obviously, mackerel icefish replace part of their diet with other prey, such as *Thysanoessa macrura*, *Themisto gaudichaudii*, mysids or other crustaceans when krill is not sufficiently available (Kock et al. 1994). In the Elephant/South Shetland Islands region, the constant

predominance of krill in the diet suggests that its availability for *C. gunnari* is not limited there during austral summer.

#### Feeding intensity

The high feeding intensities observed during the three years of this investigation support the notion that *C. gunnari*'s major food source was not limited. Most of the stomachs analysed were more than 25% full in all the three years. This suggests that the fish had fed the night prior to capture, based on an estimated digestion time of 36–48 h (Kock 1992). The average time span between food intake and capture was probably smaller in 2002 and 2003 than in 2001, as indicated by the distribution of degrees of digestion.

Some variability in feeding intensity was indicated by a higher proportion of empty stomachs in 2002. Similarly high portions of empty stomachs were reported at South Georgia in the years when the availability of krill was low (Kock et al. 1994), or at Elephant Island in the austral winter, when feeding intensity seemed to be low and less krill was available (Gröhsler 1992). It is possible that the higher proportion of empty stomachs in 2002 reflected a reduced availability of *E. superba* on a local scale.

The feeding intensity of *C. gunnari* can vary extensively both on a temporal and a spatial scale (Kock et al. 1994). The overall biomass density of krill at Elephant Island was higher in 2001 than the long-term average (Thomasson et al. 2002), which may have resulted in maximum feeding activity of mackerel icefish in that summer. Data on krill biomass from 2002 and 2003 were not available at the time of the present investigation. The grid of the regular AMLR and "Polarstern" surveys in the region in summer (15 nm distance between sampling stations) appears to be too coarse to adequately reflect small-scale differences in the abundance of krill for the purpose of a feeding study.

#### Quantitative food intake

In *C. gunnari*, there was a moderately exponential increase in stomach content weight with increasing body size in all three years. An exponential model could be fitted to the data of each year separately. However, the relationship of fish length with stomach content weight seemed to vary considerably between years, as indicated by the different model constants, *a* and *b*.

The positive correlation of stomach content weight with the size of fish was reflected by a similar trend in the daily rations. Mean daily rations per individual in 2001 and 2002 were at the upper end of the range reported by other authors, which were from between 0.1 g and 1.2 g per day (Gröhsler 1992) to 3.0 g per day (Duhamel and Hureau 1985). In 2003, they were significantly above these values. The mean daily ration is dependent on the size composition of the investigated



fish. Thus, results from different investigations are hardly comparable if the size compositions of the sampled fish are not similar.

Daily feeding rates ranged from 1.0% to 1.5% body weight in the three years of the investigation. They were well within the expected range for notothenioids, which was 0.5% to 2.5% of total fish weight per day (Kock 1992), as well as close to previous approximations ranging between 0.5% (Gröhsler 1992) and 2.2% body weight per day (Duhamel and Hureau 1985). In 2002, the feeding rates in fish shorter than 30 cm were significantly lower than in the larger animals. Almost 50% of these smaller *C. gunnari* were caught at three stations located close to each other north of Livingston Island. This observation probably reflects a local effect due to a low availability of prey in that area.

Daily rations and feeding rates were derived from a general model on the course of feeding and digestion which can only provide a rough approximation. A number of mathematical models have been developed to describe gastric evacuation over time (Bajkov 1935; Windell 1966; Elliott and Persson 1978; Jobling et al. 1977; Persson 1986; Dos Santos and Jobling 1995; Andersen 1999, 2001). Almost all of these experimental studies were conducted on fish from temperate or warm waters. Only Hop and Tonn (1998) provided extensive experimental data on digestion rates in cold-adapted arctic cod. Since channichthyids are difficult to keep under laboratory conditions, no data were yet available on their digestion rates based on feeding experiments. Experiments on other notothenioids have been conducted by Crawford (1978), Montgomery et al. (1989) and Boyce et al. (2000). The latter two reports suggest that an exponential model of gastric evacuation can be helpful in realistically estimating feeding rates of *C. gunnari*.

Previous estimates of daily rations and feeding rates of mackerel icefish from field data were obtained with a variety of methods, ranging from the calculation of a mean daily stomach content weight to various gastric evacuation models (Taverdieva 1982; Naumov et al. 1983; Duhamel and Hureau 1985; Gröhsler 1992). Our results were within the range reported by these authors, with the exception of Taverdieva (1982) who reported much higher daily rations and feeding rates. However, these were far outside the usual range estimated for notothenioids (Crawford 1978; Naumov et al. 1983; Montgomery et al. 1989; Pakhomov and Tseitlin 1992) and should be considered with caution.

The krill consumption by *C. gunnari* in the area of investigation was between 700 mt and 1200 mt per month in 2001–2002, and probably considerably higher in 2003 because of higher feeding rates in that year. In all three years, krill consumption was significantly above the values calculated by Gröhsler (1992) for the Elephant Island area in early winter 1986. As mentioned above, seasonal effects can strongly influence the diet composition and feeding intensity of *C. gunnari*. For this reason, we did not use the data to calculate the annual

krill consumption because too little is known about the feeding of mackerel icefish throughout the rest of the year.

The importance of *C. gunnari* as a major predator on krill in the region has declined significantly since the depletion of the stock in the late 1970s. The stock was most likely an order of magnitude larger than today (Kock 1992), and so was its impact on krill in the area. Whether this decrease in the population of *C. gunnari* has had a positive effect on krill populations or concurring predators would be an interesting question for future investigations.

### *Chaenocephalus aceratus*

#### *Diet composition*

In *C. aceratus*, a change in feeding behaviour was apparent at a length of 30–35 cm. At this stage, the composition of the diet changed gradually from crustaceans (mostly krill and mysids) to demersal fish. This observation is also supported by earlier results of Siegel (1980) who found that the infestation rates of endoparasitic nematodes that typically have fish as intermediate hosts increased from less than 20% to 100% in *C. aceratus* 30–35 cm in length.

In the 2001 data, the ontogenetic shift in diet composition could be illustrated by the dietary coefficient  $Q$ , although  $Q$  values calculated separately for small and large fish suggested that crustaceans were still important in larger animals. The observed similarity of the species composition of fish found in stomachs and trawl catches in all three years suggests that large *C. aceratus* are opportunistic and take what they can get, including crustaceans.

Data on the diet of *C. aceratus* are scarce. Most previous studies were based on a limited number of samples since a large proportion of stomachs was usually empty. The results also varied in the manner they were presented: numerical (Kock 1981; Kozlov et al. 1988), gravimetric (Takahashi and Iwami 1997) or both (Gröhsler 1992). However, our findings suggest that the exclusive application of either numerical or quantitative methods can be misleading with respect to the importance of different food items in *C. aceratus*. A dietary coefficient, such as  $Q$ , can enhance the comparability of different sets of data if the food composition is heterogeneous (Hyslop 1980).

On the basis of this coefficient, crustaceans and fish turned out to be almost equally important to the diet of Scotia Sea icefish on an overall view. Our results were within the range of the above mentioned investigations, if it were taken into account that the proportions of crustaceans and fish can fluctuate considerably between different years as well as between different areas of investigation (Kock 1981; Kozlov et al. 1988; Takahashi and Iwami 1997). These fluctuations could either be due to changes in the availability of one or both prey types,

or to differing size compositions of the *C. aceratus* investigated.

### Feeding intensity

In *C. aceratus*, a high proportion of empty stomachs is a common phenomenon (Kock 1981; Gröhsler 1992; Casaux et al. 2003). It has been suggested that a large proportion of Scotia Sea icefish regurgitate when they are caught (Kock 1981; Gröhsler 1992). In contrast, few stomachs with signs of regurgitation, such as reversed or expanded stomach walls, were found in this study, implying that *C. aceratus* fed very infrequently. However, this deduction should still be viewed with caution because it cannot be excluded that stomachs re-contract quickly after regurgitation.

### Stomach content weight

The change in the diet from small crustaceans to demersal fish is accompanied by a remarkable rise in the stomach content weights of fish larger than 30 cm. Because of considerable variability in the sizes of the ingested fish, stomach content weight fluctuated considerably in larger Scotia Sea icefish in all three years. These fluctuations made it impossible to fit the data adequately to a model describing the relationship between stomach content weight and fish length, even if the records from three years were pooled together.

### Conclusions

*Champscephalus gunnari* and *Chaenocephalus aceratus* represent two different lifestyles within the family Channichthyidae which are clearly reflected both by diet composition and feeding intensity. Both species are known to take advantage of planktonic crustaceans, primarily *E. superba*. However, they differ significantly in the extent to which they use this resource.

In the course of evolution, *Champscephalus gunnari* has developed adaptations supporting the exploitation of midwater resources, such as a more streamlined body shape and reduced buoyancy compared to other channichthyids of the seasonal pack-ice zone (Eastman and Sidell 2002). The early life stages of mackerel icefish are pelagic (Frolkina 2002). After attaining sexual maturity, they change to a more semi-pelagic mode of life. They undertake regular diurnal migrations into the water column, where they feed mainly on euphausiids, becoming more demersal the older they get (Duhamel and Hureau 1985; Trunov et al. 2000; Frolkina 2002). The Elephant/South Shetland Islands region provides an unlimited availability of krill during the austral summer, thereby supporting high feeding intensities and a continuous mode of food intake.

Like their planktivorous sister species *Champscephalus gunnari*, *Chaenocephalus aceratus* up to a size of

30–35 cm seem to take advantage of small crustaceans. They gradually feed more on demersal fish the larger they become. For young *C. aceratus*, there is nothing as abundant, as high in energy and as easy to catch as krill and mysids (Clarke and Prince 1980; Siegel 2000). A switch to a demersal, more piscivorous mode of life is probably advantageous for older animals: although fish are less abundant, they can deliver a large amount of energy once they are caught. An energy-saving, ambush-feeding mode of life, as indicated by behavioural observations (Daniels 1982) would be appropriate to perform such a feeding strategy.

**Acknowledgements** We thank the crews of R.V. 'Yuzhmoregeologiya' and R.V. 'Polarstern' for their excellent support on board. Special thanks go to the US AMLR program for logistic help.

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